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Abstract

We describe a novel method to estimate the probabilities of maturing at age as a function of size; these probabilities can often be interpreted as probabilistic reaction norms for age and size at maturation. Such estimations are useful for describing maturation process independently from the processes of growth and mortality, and they can also help to disentangle phenotypic plasticity from evolutionary changes in maturation. The estimation method can be used when mature and immature individuals are representatively sampled over two consecutive seasons, even when maturing individuals are not distinguished. Confidence intervals are derived for the reaction norm parameters using a bootstrap approach. Using simulated data, the method is shown to be asymptotically unbiased and robust to moderate violations of the main simplifying assumptions. However, it is relatively sensitive to small sample sizes: the method is not robust when fewer than about 100 individuals (mature and immature) are sampled from a cohort at a certain age. The method is illustrated by an application to Georges Bank cod stock (*Gadus morhua*) but can be used for any type of organism.

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Estimating reaction norms for age and size at maturation when age at first reproduction is unknown

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ABSTRACT

We describe a novel method to estimate the probabilities of maturing at age as a function of size; these probabilities can often be interpreted as probabilistic reaction norms for age and size at maturation. Such estimations are useful for describing maturation process independently from the processes of growth and mortality, and they can also help to disentangle phenotypic plasticity from evolutionary changes in maturation. The estimation method can be used when mature and immature individuals are representatively sampled over two consecutive seasons, even when maturing individuals are not distinguished. Confidence intervals are derived for the reaction norm parameters using a bootstrap approach. Using simulated data, the method is shown to be asymptotically unbiased and robust to moderate violations of the main simplifying assumptions. However, it is relatively sensitive to small sample sizes: the method is not robust when fewer than about 100 individuals (mature and immature) are sampled from a cohort at a certain age. The method is illustrated by an application to Georges Bank cod stock (*Gadus morhua*) but can be used for any type of organism.

Keywords: reaction norm, phenotypic plasticity, probability of maturing, robustness assessment, maturation dynamics

INTRODUCTION

Maturation is one of the most important ontogenetic transitions in an individual's life. It marks the start of the reproductively active part of the life cycle. Maturation has an effect on growth through changes in energy allocation and behaviour. Maturation also influences mortality risk later in the life, both because of behavioural changes and growth-mediated effect on size-at-age. Knowledge on how environmental factors influence age and size at maturation is consequently essential for understanding how populations react to anthropogenic and natural changes in their environment. Furthermore, since maturation influences fertility, growth and mortality, fitness is sensitive to change in age and size at maturation (Roff, 1992; Stearns, 1992). Consequently, understanding the causes and the consequences of variations in age and size at maturation is of great importance for both demographic and evolutionary studies.

Age and size at maturation are clearly not independent traits, i.e. change in one generally results in a correlated change in the other (Roff, 1992; Stearns, 1992). The co-dependence of maturation on age and size is described by the reaction norm for age and size at maturation that, in its original, deterministic form, gives the combinations of age and size at which maturation occurs (Stearns and Koella, 1986). In general, reaction norms describe how one genotype can give rise to distinct phenotypes when exposed to different environmental conditions (Fig. 1A). In particular, the reaction norm for age and size at maturation describes how variability in growth conditions, reflected by variations in size-at-age, influences maturation (Fig. 1B). Notice that variations in environment appear only indirectly as variations in growth in this reaction norm description. As a consequence, the reaction norm terminology is only warranted for the population level descriptions when variations in growth are mostly caused by environment rather than genetic differences between individuals.

In real data, age and size at maturation tend not to be confined to a single curve but instead show varying degrees of scatter. This variability is not accounted for by the original maturation reaction norm concept by Stearns (Stearns and Koella, 1986). To deal with the inherent stochasticity in the maturation process, Heino et al. (Heino *et al.*, 2002b) proposed a refined probabilistic definition for the maturation reaction norm, in which the reaction norm is defined as the probability an immature individual maturing, during a certain age interval, expressed as a function of age and size. In this paper we operate in the domain of the probabilistic definition. Probabilistic reaction norms are best illustrated by their contour lines, e.g., by the midpoint, which is the size at which probability of maturing is 50% at a certain age.

The probabilistic reaction norm for age and size at maturation can be estimated with simple logistic regression if representative data describing the age and size of both newly matured and immature individuals are available (Heino *et al.*, 2002a). However, for many populations the data describing the size and age of either immature or newly matured individuals are missing. The first case may arise when immature and mature parts of the population are spatially segregated. In this case it may still be possible to estimate the reaction norm by reconstructing the missing data (Heino *et al.*, 2002a). The second case arises when the newly matured individuals cannot easily be distinguished from those that matured earlier.

In this paper we present a novel method to estimate reaction norms for age and size at maturation. The specific advantage of the method is that it can be applied even when data on age and size at maturation are unavailable. Instead, the new method is based on comparing proportions of mature individuals at age and size at two consecutive time intervals (e.g., seasons). In other words, the method requires two “snapshots” of data from a population, and the maturity status, age and size of the sampled individuals to be determined. As no direct information on the actual maturation events are required, the method is ideally suited for studying temporal and geographical variations in maturation. We will first show how probabilistic reaction norms can be estimated with our novel method. As an example, we apply the method to cod (*Gadus morhua*) on Georges Bank.

THE NEW ESTIMATION METHOD

In this section we derive our method to estimate reaction norms for age and size at maturation. We will first present an outline of the method, followed by the detailed description of the various steps in the estimation procedure.

Our method is based on estimated proportions of mature individuals as functions of age and size. We will adopt the convention of referring to these proportions as “maturity ogives”, which is a term commonly used in fisheries science. For the sake of clarity we assume that growth and survival are identical among immature and maturing individuals within an age-class. Furthermore, growth is assumed to be independent of size within an age-class. These assumptions are critically evaluated later (see the Discussion); the assumptions could also be relaxed if necessary data were available. For generality, we use the term "size" throughout the paper. In practice, the measured variable is often the body length, but it could also be weight or any other variable measuring the accumulation of biomass along life.

Deriving the probability of maturing from maturity ogives

The goal of the estimation is to estimate probability of maturing as a function of both age and size for a certain cohort of individuals. However, the idea of the method is easier to grasp by first ignoring size, i.e., by considering how probability of maturing at a certain age is calculated from an age-specific maturity ogive. This calculation is then extended to account for size as well as age.

Proportion of mature individuals at a certain age a is the sum of the proportion mature in the previous age and the contribution from the influx of newly matured individuals. The latter is the product of the proportion of immature individuals that could potentially mature and the probability of maturing at age a. Thus,

$$\mathrm{P}(\text{mature at age } a) = \mathrm{P}(\text{mature at age } a\text{-}1) + \mathrm{P}(\text{not mature at age } a\text{-}1)\,\mathrm{P}(\text{maturing at age } a \mid \text{not mature at age } a\text{-}1),$$

where P denotes probability. This equation can be expressed in a more compact form if the conditional probability of maturing is denoted with $m(a)$, and the probability of being mature, given by the maturity ogive, with $o(a)$ (Heino *et al.*, 2002a):

$o(a) = o(a-1) + m(a)(1-o(a-1))$.

For the sake of simplicity we refer, through out the paper, to *m* (and maturation reaction norms) as the probability of maturing but it must be emphasised that it is the probability of maturing conditional to not having matured at an earlier time interval, and to being alive. By rearranging this equation, the age-specific probability of maturing can be expressed as a function of maturity ogives:

$$m(a) = \frac{o(a) - o(a-1)}{1 - o(a-1)}. \quad (1)$$

Extension of equation (1) to account for both age and size is straightforward, requiring only two amendments. First, one needs to consider maturity ogives that give the probabilities of being mature as a function of both age and size (*s*), denoted with $o(a,s)$. Second, in the indexing for size, one needs consider how the size of an individual changes between age $a-1$ and *a*. Here we assume that all individual within an age class have identical annual growth increments, $\Delta s(a)$. Thus, the age- and size-specific analogue of equation (1) is

$$m(a,s) = \frac{o(a,s) - o(a-1, s-\Delta s(a))}{1 - o(a-1, s-\Delta s(a))}. \quad (2)$$

This equation corresponds to the intuitive idea that to derive the probability of maturing at age *a*, we have to: (1) subtract the number of individuals that were already mature at age (*a*-1) from the number of individuals that are now mature, (2) divide the result by the number of individuals that were not mature at age (*a*-1) in order to get a probability, and (3) take into account the growth of individuals.

Calculation of maturation probabilities with equation (2) relies on two simplifying assumptions (see the Appendix): immature and mature individuals of a given size have the same age-specific growth and survival rates. Under these assumptions, in order to calculate the reaction norm

for age and size at maturation, one needs to estimate two objects: maturity ogives at age and size, $o(a,s)$, and growth rates at age, $\Delta s(a)$.

The precision of the reaction norm estimation could potentially be improved if growth could be estimated as a function of both age and size. However, estimating the size dependence of growth is often not possible with available data, which only allow for the estimation of growth rates as population scale averages. Similarly, it would be a priori desirable to take into account the inter-individual variability in growth. Preliminary analyses showed that taking the standard deviation of growth into account increment modifies only marginally the reaction norm estimations. Thus, only the simpler method is presented here. Moreover, preliminary tests showed that the estimation method is not very sensitive to growth estimations.

Estimation procedure

We have shown in the previous subsection how the maturation reaction norm can be calculated when age- and size-specific maturity ogives and age-specific growth increments are known. In this section we present the statistical procedures needed, first, to estimate the required ogives and growth increments, and, second, to use these quantities to estimate the maturation reaction norm.

Estimation of age and size-based maturity ogive

Maturity ogives at age and size are estimated using annual samples, collected at a time where age and maturity status can be determined. The most elementary approach is to compute the percentages of individuals that are mature separately for each age and size class. However, a more robust approach is to use some parametric function with size and age as explanatory variables. Here we use logistic regression models (Collett, 1991). Although there is no particular mechanistic underpinning the choice of logistic regression models, experience shows they fit data well (Jørgensen, 1990; O'Brien, 1999); other types of curves can readily be used if they fit particular data better than the logistic curve.

Since the reaction norm that we want to derive is the property of a given stock at a given time, probabilities of being mature are to be computed separately for different cohorts. No a priori assumption is made on the effect of age on maturation. Consequently, the following model is fitted independently for each cohort and age:

$$\text{logit}(o) = \ln\ \frac{o}{1-o}\ = c_0 + s \times c_1\text{, (3)}$$

where $\text{logit}(o)$ is the logit link function and c_0 and c_1 are the parameters to be estimated. The estimated model is then used to calculate probabilities of being mature for any age or size that are required when applying equation (2). The estimated model allows also interpolation to size classes where actual observations are missing; such predictions, however, may not be robust.

Growth rate

Growth rates can be estimated using any available method. The simplest way is to use the same data set as for the ogive estimation: with annual samples of aged and sized individuals, one can compute a mean size at age for each cohort. Growth rate at age for each cohort is then estimated by subtracting the means of consecutive years. Alternatively, growth increments can be estimated from growth trajectories of individuals when such data are available.

Reaction norm

When probabilities of being mature and growth rates have been estimated using respectively logistic regressions and differences of mean sizes at age (see above), the probabilities of maturing within the observed range of ages and sizes are calculated using equation (2). These probabilities constitute “raw” reaction norms. However, the use of equation (2) may occasionally lead to unrealistic results: the computed probability of maturing may become negative, or may decrease with size. These problems are particularly prone to occur when the sample size is low and probabilities of being mature are very high or very low. One may need to conclude that insufficient data prevents the estimation of the reaction norm for particular age and cohort combinations.

The raw reaction norms are fully determined by the parameters of the estimated statistical models for the maturity ogives and the annual growth increments. However, if these reaction norms display a sigmoid dependence on size, fitting a logistic regression model provides a simple parameterisation for the reaction norm. Moreover, such parameterisations facilitate comparisons of the reaction norms among different cohorts or stocks. Here we use the following logistic model for each cohort and each age to parameterise the reaction norm:

$$\text{logit}(m) = d_0 + s \times d_1 . \quad (4)$$

These models fully describe the reaction norm, however, it can be useful to summarise the information for illustrative purposes or for comparison of the maturation of different cohorts or ages. One possibility is to display contours on which the probability of maturing takes particular values, e.g. the midpoint (m=0.5), or the quartiles (m=0.25, and m=0.75). The midpoint, denoted by $S_{50,}$ is calculated by replacing m by 0.5 in equation (4):

$$S_{50} = \frac{-d_0}{d_1} .$$

The quartiles are calculated similarly:

$$S_{25} = \frac{-\ln(3) - d_0}{d_1} \text{ and } S_{75} = \frac{\ln(3) - d_0}{d_1} .$$

We emphasise that the midpoint is not the size at which 50 % of individuals actually mature. The midpoint only specifies the size at which the probability to mature is 50 %, with no reference to abundance of cohort at that size class. At young ages, most (or even all) individuals may be smaller than that size, which would mean that only a small proportion of a cohort is expected to mature at these ages (see Fig. 2).

The size at which probability of maturation is 50% (S_{50}) is not to be confused with the so-called L_{50}, the size at which 50% of individuals are mature. The latter is a frequently used descriptive statistic in fisheries science which is usually not age-specific (Chen and Paloheimo, 1994; O'Brien, 1999). In contrast, the reaction norm midpoint is always age-specific.

Estimation of confidence intervals

The estimation procedure presented above does not yield directly applicable measures of uncertainty in parameter estimates of the reaction norm. Furthermore, no statistical inference can be based directly on the final logistic regressions that describe the reaction norms. The problem arises from the fact that the probabilities of maturing are not directly based on observed data. Instead, they are computed with a complex non-linear function of growth rates and maturity ogives, which are predictions from another statistical model. We solve this problem by using bootstrap techniques to derive confidence intervals for the reaction norms (Manly, 1991): bootstrap confidence intervals are derived by resampling the observed samples. To construct a bootstrapped sample for each age and cohort, individuals are chosen at random with replacement. The final bootstrapped sample contains an equivalent number of observations as in the original sample. The resulting resampled data set is used to estimate the maturity ogives and the growth rates and then to derive the reaction norms of the different cohorts and their parameters. The resampling is repeated 1000 times, and the distribution of the estimated parameters is used to derive confidence intervals with the first percentile method (Manly, 1991).

ROBUSTNESS OF THE ESTIMATION METHOD

It is important to ascertain the validity of our method when it is applied to empirical data. Is it robust to low sampling sizes? Is it robust to the violation of the assumption that immature and mature individuals have the same growth and survival rates? To answer these questions we use simulated data. Maturation dynamics is simulated using a known probabilistic reaction norm, and the resulting data sets are then used to estimate the reaction norm with our method. Below, we first describe how artificial data sets are built, and then present two types of robustness tests: robustness to small sample size, and robustness to the simplifying assumptions used to derive equation (2).

Building artificial data sets

Our robustness assessment is motivated by the example of Georges Bank cod stock that is presented in the next section. We assume in the simulations a very large initial cohort size (N_{cohort}=100000). The chosen value for the cohort size is much smaller than in reality, but this choice does not influence the robustness assessment as long as the cohort size is large enough to avoid any significant demographic stochasticity (Caswell, 2001). Data are generated allowing individuals to mature according to a given probabilistic reaction norm for age and size at maturation and to grow deterministically. Each year a fixed number of individuals are sampled (N_{sample}); the sample size will be varied in the subsequent robustness tests. The estimated reaction norms for the GB cod are close to horizontal; for illustrative purposes we use a horizontal reaction norm with all midpoint values equal to 50 cm (size at which the probability of maturing is 0.5) and an inter-quartile range of 10 cm. The following procedure is used to generate the artificial data sets:

1. The size (s) distribution of immature individuals, $n_I(s,a)$ at the first considered age (a=1) is generated for the N_{cohort} individuals. Sizes are randomly picked from a normal distribution with mean length 10 cm and standard deviation 5 cm. The size distributions of mature individuals, $n_M(s,a)$, are initially empty.
2. The probability of maturing is determined using the reaction norm. Maturing individuals are chosen randomly according to this probability and are then transferred to the size distribution $n_M(s,a)$. Non-maturing individuals are kept in the immature size distribution $n_I(s,a)$.
3. N_{sample} individuals are chosen randomly from the two pooled distributions ($n_M(s,a)$ and $n_I(s,a)$). They constitute the output data for one age.
4. Immatures and matures survive with probabilities $\sigma_I(s)$ and $\sigma_M(s)$. Unless stated, we always considered $\sigma_I(s)=\sigma_M(s)=\sigma$. The exact value of σ=0.85 does not matter as long as enough individuals survive to avoid sampling errors.
5. Immatures and matures grow according to a von Bertalanffy curve using parameters (K=0.12, L_∞ =148.1, t_0=-0.616) estimated for Georges Bank cod stock (Penttila and Gifford, 1976).

Unless stated otherwise, mature and immature growth rates are considered equal. The obtained immature and mature distributions are transferred to the next age.

Each iteration of steps 2 to 5 generates data for one age. Iterations are repeated until the immature and mature size distributions at age 5 have been computed and sampled. The final output data set is then composed of N_{sample} mature and immature individuals at each age. This type of data set enabled to apply exactly the method described above (in the section *The new estimation method*) to estimate the maturation reaction norm. Five replicate data sets are computed for each robustness test to determine whether errors in estimations are systematic or not. Differences between the theoretical and the estimated reaction norm are assessed using the midpoint (S_{50}), the inter-quartile range (S_{75}-S_{25}), and the slope of the linear midpoint-age regression, as descriptive statistics. The mean and the mean absolute error for these three parameters are displayed in Tables 1 and 2. We also analysed the shape of the estimated reaction norm using the quadratic coefficient obtained by quadratic age-midpoint regression.

Results of the robustness tests

To test whether the method is valid and to determine the required sample size, we first check for the existence of any systematic bias and a possible link between such a bias and the sample size. Six sample sizes are used: 1000, 500, 250, 100, 50, and 30. At large sample sizes (500 and 1000) sampling errors are minimal, and estimated reaction norms are very similar to the theoretical ones (Table 1 and Fig. 2). Errors in the estimated midpoints, inter-quartile ranges and slopes increase when sample size decreases but the bias is not directional: these quantities are stochastically underestimated or overestimated due to sampling errors. As shown in Figure 2, errors are more likely to arise and are higher for ages at which few individuals mature (at points of the reaction norms that are away from the intersection with the mean growth curve) than for ages at which most individuals mature. This can lead to large errors in the estimated slope at low sample size, although the shape of the central part of the reaction norm is correct (see Fig. 2, sample size=100). When sample size is low (50 or 30) it is

often impossible to compute the reaction norm midpoint for ages at which few individual actually mature. These problems result from the fact that at ages where few individuals mature, either immature (age 5) or mature (age 1) individuals are so rare that they are unlikely to be sampled. Samples that contain very few immature or maturing individuals do not contain enough information to robustly estimate the parameters of logistic regressions that are used to describe the maturity ogive.

The bootstrap approach provides 95% confidence intervals for the midpoint estimations (Fig. 2). Confidence intervals are generally less than 5 cm wide when the sample size is high enough. They are always the narrowest at age 3, where the majority of individuals mature (see estimated growth curve on Fig. 2). They are wider at age 1. At low sample sizes (n=50) confidence intervals are so wide that the validity of the estimation is questionable. This is not unexpected given that sampling error depends on sample size. Moreover, the use of bootstrap becomes itself problematic. As explained above in the estimation procedure section, maturity ogives are validly estimated when enough mature and immature individuals with enough variability in their size are sampled at each age. When the observed data set is resampled in the bootstrap procedure, there is no guarantee that the qualitative properties of the original data set are retained. For example, bootstrap samples might contain only immature or mature individuals even when the original sample contains both immature and mature individuals. When sample size decreases, convergence problems and high standard deviations for estimated parameters are more likely. This leads to wide confidence intervals for the reaction norm midpoints, and to non-normal bootstrapped distributions (the confidence intervals are highly skewed toward values that are higher than the observed value, see Fig. 2, sample size 50). In extreme cases (at very low sample size, or at ages where few individuals mature) it is even not possible to compute the reaction norm for some bootstrapped data set. For example, for sample size 50, and age 5 (Fig. 2), only 79 replicates out of 1000 bootstrapped samples led to a successful estimation of the reaction norm midpoint. The validity of the confidence interval is thus highly questionable.

We then assess the robustness of the estimation method to the two assumptions needed to derive maturing probabilities (equation 2): immatures and matures have the same growth and survival

rate. We thus generated data sets assuming that mature individuals have a higher survival rate than immature ($0.75\ \sigma_I(s) = \sigma_M(s)$), or vice versa ($\sigma_I(s) = 0.75\ \sigma_M(s)$). Alternatively, we generate data sets assuming that mature growth rate is 0.75 times higher or smaller than immature growth rate. Finally, the joint effect of the violation of the two simplifying assumptions is tested. An artificial data set is built supposing that mature individuals grow 25% slower than immature, and that mature individuals have a higher survival rate than immature ($0.75\ \sigma_I(s) = \sigma_M(s)$), and vice versa ($\sigma_I(s) = 0.75\ \sigma_M(s)$).

When sample size is very large (n>500), the violation of the assumption of equal growth rates or equal survival probabilities is inconsequential: the bias in the estimated reaction norms is negligible. Significant biases arise only when samples are small. Absolute errors in the midpoints, in the inter-quartile range, and in the slope increase when sample size decreases from 500 to 100 (in most cases they roughly double). Errors, especially in the reaction norm slope, are slightly higher when the hypothesis of equality between mature and immature growth rates is violated, than when the hypothesis of equality between mature and immature mortality rates is violated (Table 2, comparison between rows A-B and C-D). The violation of these two assumptions at the same time does not lead to higher estimations errors: biases are not cumulative (Table 1, comparison between rows A-B-C-D and E). Higher mortality after maturation results in overestimating the midpoints and to positive reaction norm slopes while it is the reverse for lower mortality after maturation. Higher or lower growth rate after maturation does not lead to a consistent over- or under-estimation of the reaction norm midpoint and slope across sample sizes (comparison of the Table 2 cells for n=100 and n=500). The violation of the two hypotheses (either considered separately or not) leads to an overestimation of the inter-quartile range (just one exception).

The robustness tests do not indicate any significant systematic bias in the shape of the estimated reaction norm. Yet, six artificial data sets out of 80 led to a statistically significantly convex reaction norm. Furthermore, when curvature is not significant, the estimated reaction norms tend to be slightly convex when judged visually (Fig. 2, n=100). This issue is due again more to problems of sample size than to the estimation method in itself: estimated reaction norms are sometimes slightly

convex because estimation problems arise at low sample size and at ages where few individuals mature. Thus, the reaction norm midpoints tend to be underestimated at age 1 and age 5 and the reaction norm are slightly convex.

APPLICATION TO THE GEORGES BANK COD

As an illustrative example, the method we have described is used to estimate the reaction norm for age and size at maturation for the Georges Bank stock of Atlantic cod (*Gadus morhua*); a full analysis will be presented in a forthcoming paper. The data are obtained from the spring bottom trawl survey conducted since 1968 by the Northeast Fisheries Science Center along the Northeast coast of the USA (Azarovitz, 1981; O'Brien, 1999). An average of 299 fish are sampled each year, i.e. about 60 individuals at age. Biological sampling is random and length stratified. Age, length and maturity status are determined routinely so that maturity ogives, growth rates, and probabilities of maturing at age and size can be computed using the methods described above. We directly compute the probability of being mature as a function of both age and size using a single logistic regression model, without weighting by abundance at length (Morgan and Hoenig, 1997). To increase sample sizes, males and females are pooled, which is usually not a safe option, but preliminary computations showed us here that male and female maturation reaction norms are only slightly different.

Computing the probability of maturing proved to be generally unsuccessful when there are less than ten mature individuals, or less than ten immature individuals sampled at age for a given cohort. For this reason computing the probability of maturing for ages 1 and 5 when few individuals are maturing is not possible. Moreover, estimating maturity ogives using a logistic regression also requires that sampled mature and immature individuals have sufficiently contrasting sizes at the considered ages. We conclude that in order to safely compute the reaction norms the estimation has to meet the following conditions: (1) The logistic regression for the ogive is statistically valid (convergence of the estimation process, and low standard deviations for the estimated parameters). (2) The probabilities of maturing, computed using the estimated maturity ogives, are increasing with size.

(3) The observed size range allows computing the midpoint of the reaction norm by interpolation, or by extrapolation using another logistic regression if the midpoint is not too far from the observed range. As a consequence of these requirements, it is possible to compute the probability of maturing at age and size for ages 2, 3 and 4 and only in a few cohorts.

Figure 3 displays the estimated probability of maturing at age 3 for two cohorts (1969 and 1983) and the fitted logistic regression curve. It describes the way these curves are used to compute the reaction norm midpoints, i.e. the link between the probability of maturing at a given age as a function of size and the reaction norm for age and size at maturation. As an example Figure 4 displays the midpoints of the reaction norm for age 3 and the cohorts 1969, 1975, 1980, 1983, and 1996, as well as the corresponding inter-quartile ranges. Small sample sizes preclude computation of midpoints for the other cohorts. Bootstrapped 95 % confidence intervals are also displayed for the reaction norm midpoints. Midpoints vary between 38.9 and 48.9 cm. The confidence intervals for these midpoints are all between 5 and 7 cm wide. Inter-quartile ranges ranged between 8 and 14 cm. That means that a 10 cm increase in size-at-age is necessary to increase the probability of maturing from 0.25 to 0.75.

DISCUSSION

Our results show that the reaction norm for age and size at maturation can be robustly estimated from age- and size-specific maturity ogives and age-specific annual growth increments. Thus, reaction norm estimation only requires representative yearly samples of individuals for which the maturity status, age and length are determined. The method provides, therefore, an estimation of the reaction norm for age and size at maturation when newly matured individuals cannot be distinguished from those that have matured during earlier seasons – an obstacle that prevents direct estimation with simple logistic regression (Heino *et al.*, 2002a). The method presented here thus complements the method of Heino et al. (2002a) that permits the estimation of maturation reaction norms when immature individuals have not been observed.

Numerical robustness tests have proved the general validity of the method in the sense that there are no systematic errors. The method is relatively robust to the violation of the main simplifying assumptions: identical growth and mortality rates for mature and immature individuals at a certain age. Moreover, if data is available to estimate the difference in mature and immature survival rates, this difference can be taken into account in the reaction norm estimation (equation 5 in the Appendix). One drawback of the method is that it does not allow for standard statistical inference: since the estimation method is based on a non-linear equation combining results from two statistical models, it is not possible to directly derive confidence intervals for the reaction norm parameters. However, a bootstrap method is available to derive confidence intervals for the reaction norm midpoints.

The validity of the estimations, as always, depends on the quality of the data. The robustness of our method decreases significantly when sample sizes are low. Results become unreliable when less than about 100 individuals are sampled at age. Sampling error in small samples may seriously influence estimation of the maturity ogives, and consequently, it may not be possible to obtain feasible estimates of the probability of maturing. A sample size of 100 individuals at age is the bare minimum that applies when the ratio of immature to mature individuals in the sample is not very extreme. Larger samples are needed when size at age is not variable, and for ages where very few individuals are maturing. The latter case inevitably arises at ages corresponding to very early or late maturation relative to population average, constraining the characterisation of the maturation reaction norm over the whole range of maturation ages.

Sample sizes required by the reaction norm estimation method presented in this paper are so large that they are likely to restrict the use of the method in its simplest form. For example, for the Georges Bank cod the reaction norm can only be estimated for a few solitary cohorts and, therefore, an analysis of the long-term trend in maturation is hindered. The problem of insufficient sample size can be surmounted by combining data. The first option is to combine data “laterally”, from samples collected at the same time: combining males and females, different ages, or samples from different locations. The other option is to combine samples collected at consecutive seasons. By combining we

do not necessarily mean pooling all data. Data can be more efficiently combined by estimating the maturity ogives and growth increments with statistical models that use all the available data, but in which some of the interactions between the explanatory variables (e.g., age, size, cohort and sex) have been omitted. This allows a more robust estimation of maturation reactions norms with small samples by making some simplifying assumptions on the dependence of reaction norms on various explanatory variables. This method will be pursued further in a forthcoming paper. Besides, fishery data set are unique because they often encompass many years or even several decades of sampling. That was the first incentive for our work. However, sampling 100 individuals at age (at least at the ages at which individuals are likely to mature) during two consecutive years should be feasible for many organisms (animals, or trees for which age can be determined using growth rings). Obtaining estimations of maturation reaction norms and comparing the estimations for different populations should be an interesting reward for such an effort.

Simplifying assumptions of our method call for careful evaluation. In particular, the assumption that growth and survival rates are not influenced by maturation may seem far-stretched. Life-history theory predicts that reproduction results in a decrease in growth and/or survival rates because energy allocation to reproduction starts to compete with allocation to growth and maintenance (Roff, 1992; Stearns, 1992). Yet, it is difficult to demonstrate such a pattern with field data. This might be due either to practical problems or to interacting processes generally not taken into account in life-history evolution models, such as behaviour. For Georges Bank cod, no evidence has been found for a somatic cost of reproduction (Trippel *et al.*, 1995): it seems that fast growing immature individuals maintain fast growth after maturation. Similarly, demonstrating that adults have higher mortality than juveniles is difficult due to the lack of sufficiently accurate survival data. In fish, mortality change at maturation could be due to spawning migrations or other behavioural changes. Georges Bank cod, however, does not show marked spawning migration, although mortality could change due to the spawning behaviour. Nevertheless, the estimation method is relatively robust even

to large differences in between mature and immature fish survival (Table 2). For these reasons, we do not expect the estimated reaction norms (Fig. 3) to be strongly biased.

We have interpreted the estimated probabilities of maturing at age and size in Georges Bank cod as maturation reaction norms. This interpretation is strictly valid only if variations in size-at-age are mostly caused by differences in the environment experienced by individual fish, rather than genetic differences among them. However, growth is also partially genetically determined (Conover and Schultz, 1995; Wootton, 1998; Imsland and Jónsdóttir, 2002), although the relative importance of genetic factors in explaining population-level variation in natural populations is seldom known. Presence of strong genetic effects in growth does not jeopardise estimations of maturation probabilities, although it complicates their interpretation. In any case, the value of estimations of maturation probabilities is not contingent only on the reaction norm interpretation. An attractive property of probabilistic maturation reaction norms is the separation of maturation process from those of growth and mortality: because the maturation probability is expressed as being conditional to certain age and size, the process of maturation is separated from the processes of growth and survival that determine the probability of reaching that age and size (Heino *et al.*, 2002b).

Stearns and Crandall (1984) and Stearns and Koella (1986) have suggested that reaction norms for age and size at maturation can be used to separate genetic and phenotypically plastic effects on maturation. Variations in growth conditions are likely to be responsible for the bulk of phenotypically plastic within- and among-population differences in maturation in the wild. As mentioned above, the maturation reaction norm is not influenced directly by growth variations. Because reaction norms are genetically determined properties of individuals, estimation of maturation reaction norms allows the disentanglement of genetic and plastic components in maturation.

Separation of genetic and plastic components in maturation is particularly relevant for understanding changes in maturation widely observed in commercially exploited fish stocks. Most commonly, maturation occurs earlier and earlier (Rijnsdorp, 1989; Jørgensen, 1990; Morgan *et al.*, 1994; Godø and Haug, 1999; O'Brien, 1999). Three main hypotheses are advocated to explain the

decrease in age at maturation (Law, 2000). First, faster body growth could trigger earlier maturation when density-dependent effects on growth are relaxed with decreasing population size. Second, some long-term climatic trends, e.g. more favourable temperature regime, could have triggered a change in the maturation. These two hypotheses thus involve only phenotypic plasticity. Third, maturation traits could have evolved in response to selection pressures caused by fishing mortality. This explanation therefore implies genetic changes in maturation. Knowing whether changes in the maturation dynamic are easily reversible (plasticity) or not (genetic changes) is indispensable for long-term management of fish stocks.

Estimations of age- and size-dependent maturation probabilities have also other applications than disentanglement of genetic and plastic components in maturation mentioned above. In general, the maturation reaction norm allows characterisation of the maturation process in a manner that is not confounded by the processes of growth and survival (Heino *et al.*, 2002b). Estimations of maturation reaction norms can therefore greatly advance our understanding of the environmental influences on the maturation process. Notice that the commonly used probability of being mature (i.e., the maturity ogive) does not describe the maturation process itself; rather, it describes the state of a population. Furthermore, an appreciation of the need to extend the classical age-structured population models to account for size structure as well is currently mounting in the literature (Claessen *et al.*, 2000; De Leo and Gatto, 2001; Frøysa *et al.*, 2002). In the context of fisheries stock assessments, age- and size-structured models can be used in predicting stock's reproductive potential under different scenarios of future growth and mortality regimes: What is the proportion of reproducing individuals? What is their age- and size distribution? The latter point is considered increasingly important (Murawski *et al.*, 2001) as it is becoming recognised that the realised fecundity may depend, in addition to the size of reproducing individuals, also on their age distribution: at the same size older females would produce more or better quality eggs than younger females (Trippel, 1998; Trippel, 1999). In this context, the proper description of the age- and size-dependence of the maturation process is indispensable.

The estimation method can be applied to any type of population as soon as the population is sampled at least two times and individuals can be aged. Sample size requirements are probably most often met in the fisheries context where regular surveys often provide ample data. Nevertheless, the method could be applied in many studies that compare age and size at first reproduction in different populations and/or in a single population at different times and that use traditional ways to describe maturation and disentangle phenotypic and genetic differences. The maturation reaction norms could, for example be estimated to analyse spatial and temporal variations in maturation of red deer (Langvatn *et al.*, 1996), life history variations in two lizard populations (Rohr, 1997), sexual dimorphism in tortoise (Lagarde *et al.*, 2001), or metamorphosis and maturation in amphibians (Scott, 1990; Miaud *et al.*, 1999). However, the method presented here is probably not the most efficient one when individual recognition and non-destructive determination of maturity status are possible, e.g., when tagged individuals are followed, or in mark-recapture studies. With such data, maturing individuals can be identified, allowing for more straightforward estimation methods.

Taken together, the statistical method we have developed is likely to be useful to address the following types of questions: Can age and size at maturation evolve in a few generations? Are the differences in maturation between two populations purely phenotypic? What are the demographic consequences of the decrease in age and size at maturation in a given population?

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APPENDIX 1 :DETAILED CALCULATIONS OF THE PROBABILITY OF MATURING

A mathematical link between $o(a,s)$ (the probability of being mature at age *a*, and size *s*) and $m(a,s)$ (the probability of maturing at age and size) has to be derived. To do so, the survival rates of immature and mature individuals (σ_I, σ_M), as well as their growth rates (Δs_I , Δs_M) must be taken into account. Since, individuals that are mature at age *a*, are either newly mature individuals, or individuals that matured earlier and have survived till age *a*:

$$o(a,s) = \frac{\text{individual already mature at age } (a\text{-}1)\text{+newly mature individuals}}{\text{individual already mature at age } (a\text{-}1)\text{+newly mature individuals+immatures at age } a}$$

Developing this expression and noting N_I and N_M the respective numbers of immature and immature individuals and $s_M = s - \Delta s_M$, $s_I = s - \Delta s_I$ the size of mature and immature individuals at age *a-1* we get:

$$o(a,s) = \left[\sigma_M(a-1,s_M)N_M(a-1,s_M) + \sigma_M(a-1,s_M)N_I(a-1,s_M)m(a,s_M)\right] \div \left[\sigma_M(a-1,s_M)N_M(a-1,s_M) + \sigma_M(a-1,s_M)N_I(a-1,s_M)m(a,s_M) + \sigma_I(a-1,s_I)N_I(a-1,s_I)\left(1-m(a,s_I)\right)\right]$$

.

It must be noticed that this formula is derived under the hypothesis that individuals that mature the focal year and individuals that matured earlier have the same growth and survival rates, which justifies the expression for the number of newly mature individuals (second terms of the numerator and denominator).

Noting $N_T(a,s)$ the total number of individuals at age *a* and size *s* we have $N_M(a,s) = N_T(a,s)o(a,s)$ and $N_I(a,s) = N_T(a,s)\left(1-o(a,s)\right)$. Dividing the denominator and the numerator of the fraction by $N_T(a-1,s_M)$ leads to:

$o(a,s) =$

$$\left[\sigma_M(a-1,s_M)o(a-1,s_M)+\sigma_M(a-1,s_M)\left(1-o(a-1,s_M)\right)m(a,s_M)\right]\div$$
$$\left[\sigma_M(a-1,s_M)o(a-1,s_M)+\sigma_M(a-1,s_M)\left(1-o(a-1,s_M)\right)m(a,s_M)+\right.$$
$$\left.\sigma_I(a-1,s_I)\left(1-o(a-1,s_I)\right)\frac{N_T(a-1,s_I)}{N_T(a-1,s_M)}\left(1-m(a,s_I)\right)\right]$$

.

To find an expression of $m(a,s)$ as a function of $o(a,s)$, an other assumption must be made unless two unknown terms remain on the right-hand side of the equation, i.e. $m(a,s_I)$ and $m(a,s_M)$. Assuming that immatures and matures have the same growth rates at a given size, which results in s_I and s_M being equal to a common value s_* (then, we also have $\Delta s_M = \Delta s_I = \Delta s_*$), we obtain:

$$o(a,s)=$$
$$\left[\sigma_M(a-1,s_*)o(a-1,s_*)+\sigma_M(a-1,s_*)\left(1-o(a-1,s_*)\right)m(a,s_*)\right]\div$$
$$\left[\sigma_M(a-1,s_*)o(a-1,s_*)+\sigma_M(a-1,s_*)\left(1-o(a-1,s_*)\right)m(a,s_*)+\right.$$
$$\left.\sigma_I(a-1,s_*)\left(1-o(a-1,s_*)\right)\left(1-m(a,s_*)\right)\right]$$

.

After some algebra and *r* denoting the ratio $\sigma_M(a-1,s_*)/\sigma_I(a-1,s_*)$, we obtain:

$$m(a,s)=\frac{o(a,s)+o(a-1,s_*)\left(o(a,s)(r-1)-r\right)}{1+o(a-1,s_*)\left(o(a,s)(r-1)-r\right)}. \quad (5)$$

Making a last assumption, i.e. immatures and matures of a given size have the same survival rates (*r*=1) leads to:

$$m(a,s)=\frac{o(a,s)-o(a-1,s-\Delta s_*)}{1-o(a-1,s-\Delta s_*)}.$$

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Table 1: Robustness of the estimation method to small sample size. For each robustness test, corresponding to a different sample size at age, three properties of the estimated reaction norm are assessed: (a) The reaction norm midpoint that describes for each age the size at which the probability of maturing reaches 50 %. Displayed figures are averaged over all ages. (b) The inter-quartile range describes for each age the size interval within which the probability of maturing rises form 25 % to 75 %. Again displayed figures are averaged over age. (c) The reaction norm slope obtained by linear age-midpoint linear regression. Mean values are computed over five simulated replicate data sets and are displayed together with their error measured as the mean absolute difference between estimated and actual values.

1

2

	Average midpoint		Average inter-quartile range		Slope	
	mean	error	mean	error	mean	error
Actual reaction norm	50		5		0	
Estimated reaction norm						
A Sample size 1000	49.6	1.5	5.2	1.1	0.8	0.8
B Sample size 500	50.4	1.7	5.2	0.9	-0.5	0.9
C Sample size 250	49.7	3.6	5.7	1.6	-2.2	2.8
D Sample size 100	47.6	4.0	4.6	2.3	1.4	1.4
E Sample size 50	49.8	6.2	4.8	3.1	4.1	8.2
F Sample size 30	49.1	8.9	8.8	5.0	-7.9	7.9

3

Table 2: Robustness of the estimation method to the violation of the simplifying biological assumptions. The results are displayed as in Table 1 (the same three properties are used to describe the estimated reaction norms, mean and absolute mean error are given). For each robustness test, artificial data sets are used using a sample size at age of 500 and 100 individuals (respectively the first and second figure in each cell). Higher mortality after maturation (A) is realised assuming survival probabilities σ_M / σ_I =0.75, while lower mortality after maturation (B) is realised assuming σ_M / σ_I =1/0.75. Higher growth rate after maturation (C) is implemented multiplying the original growth rate by 1.25, while lower growth rate (D) is obtained multiplying the growth rate by 0.75. The cumulative effect (E) of the violations of the two hypotheses used to compute the probabilities of maturing is tested assuming at the same time that growth and survival rates decrease after maturation.

11

12

		Average midpoint		Average inter-quartile range		Slope	
	sample size	mean	error	mean	error	mean	error
Actual reaction norm		50		5		0	
Estimated reaction norm							
A higher mortality after maturation	500	51.7	3.1	5.6	1.2	0.2	0.7
	100	54.6	6.4	6.5	2.5	2.6	3.0
B lower mortality after maturation	500	49.8	1.6	4.9	1.0	-0.1	0.6
	100	49.3	4.2	6.0	2.7	-1.7	2.1
C higher growth rate after maturation	500	49.1	2.0	5.4	1.5	1.0	1.0
	100	51.8	4.0	5.0	2.0	-2.1	2.6
D lower growth rate after maturation	500	52.1	2.9	6.3	1.7	-1.6	2.4
	100	52.4	5.7	5.7	2.2	-4.8	5.6
E combination of factors	500	49.8	2.3	5.6	1.5	0.3	1.3
	100	50.2	3.5	5.5	1.7	1.5	1.6

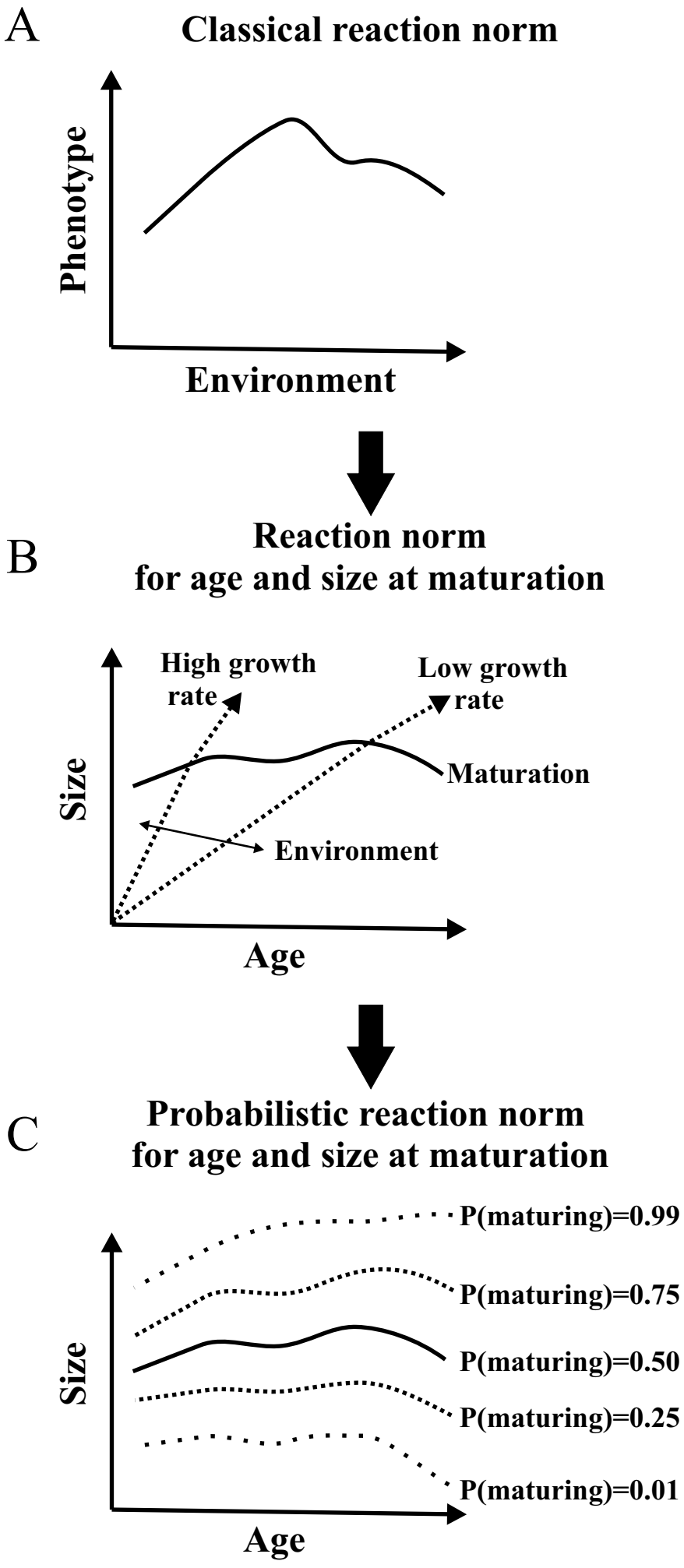
13

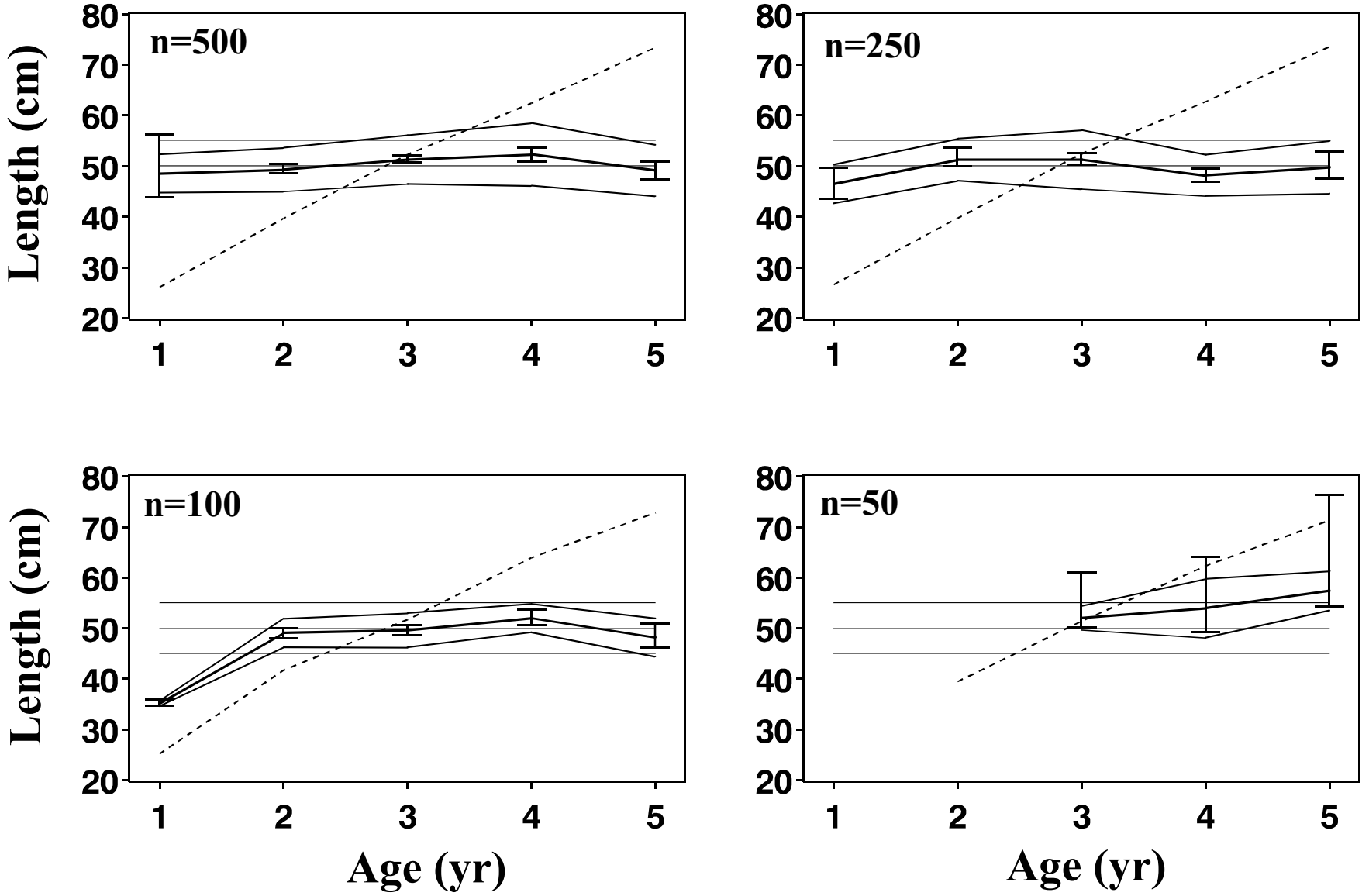
Fig. 1: Interpretation of reaction norms for age and size at maturation. "Classic" reaction norms describe the phenotypic response of an organism to environmental variability (A). Reaction norms for age and size at maturation (Stearns, 1992) give the combinations of age and size at which individuals mature (B). The interpretation of this curve as a reaction norm is based on the assumption that differences in growth curves are mediated by environmental variations. Points on the left (right) of the reaction norm correspond to high (low) growth rates presumably achieved in favourable (unfavourable) environmental conditions. Classically, all individuals are considered to mature exactly when their growth curve hits the reaction norm. Yet, maturation is a complex process that depends on factors not taken into account by age and size. Consequently the size at maturation for a given age is variable. This stochasticity is taken into account by the probabilistic extension (C) of the reaction norm for age and size at maturity (Heino *et al.*, 2002b). In this case, the reaction norm for age and size at maturation is defined by the probability of maturing at age and size, conditional on having not yet matured.

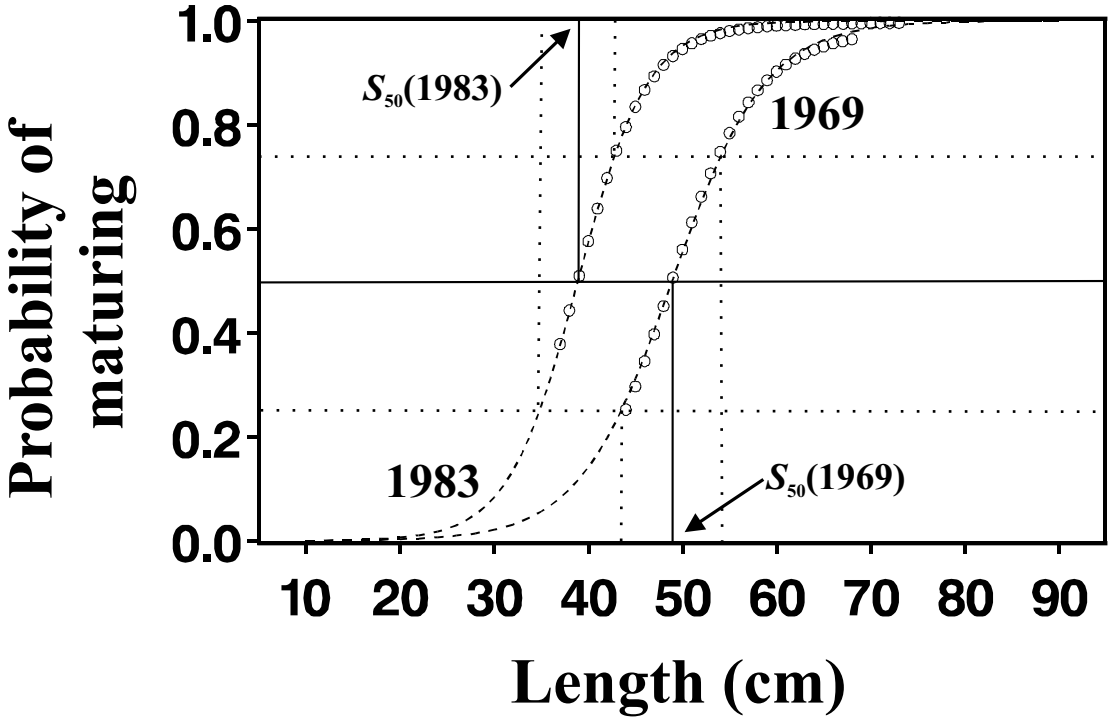
Fig. 2: Sensitivity of the estimation method to small sample sizes. Theoretical reaction norms for age and size at maturation as well as the estimated midpoints (P(maturing)=0.5) and the quartiles are displayed (P(maturing)=0.25 and P(maturing)=0.75) for four different sample sizes at age: 500, 250, 100, 50. Thin horizontal lines denote the reaction norms that are used to produce the data. Thick curves correspond to the estimated reaction norm midpoints together with 95 % bootstrapped confidence intervals. Thin curves correspond to the quartiles. Dotted lines are the mean estimated growth curves.

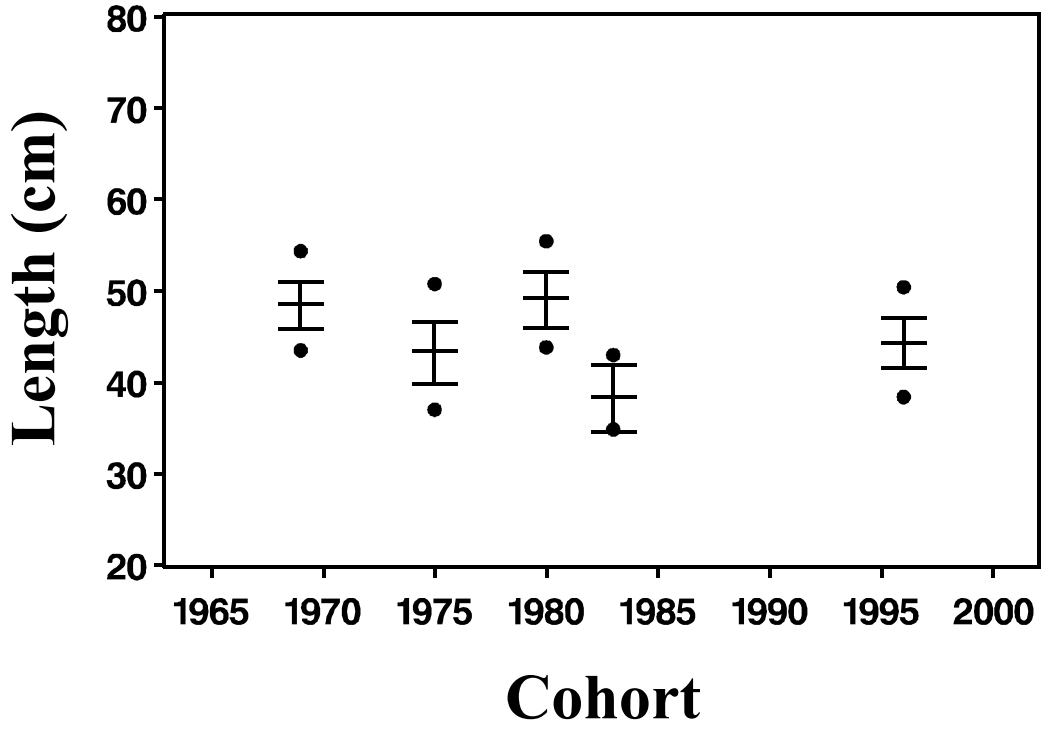
Fig. 3: Application of the estimation method for Georges Bank cod stock. Probability of maturing at age 3 computed as a function of size for the cohorts 1969 and 1983. O O O, raw estimations of the probabilities of maturing computed in the observed size range; ——, fitted logistic regression curves. Thin solid lines (doted) indicate how the reaction norm midpoints (quartiles) can be graphically determined.

Fig. 4: Application of the estimation method for Georges Bank cod stock. Reaction norms midpoints together with a bootstrapped 95% confidence interval and quartiles (dots) computed at age 3 for the cohorts 1969, 1975, 1980, 1983, and 1996. For the other documented cohorts it is not possible to estimate the reaction norm midpoints due to low sample sizes (see text for a detailed explanation).


A
Classical reaction norm
Phenotype
Environment
B
Reaction norm
for age and size at maturation
High growth
rate
Low growth
rate
Maturation
Size
Environment
Age
C
Probabilistic reaction norm
for age and size at maturation
P(maturing)=0.99
P(maturing)=0.75
P(maturing)=0.50
P(maturing)=0.25
P(maturing)=0.01
Size
Age


n=500
n=250
n=100
n=50
Length (cm)
Length (cm)
Age (yr)
Age (yr)
80
70
60
50
40
30
20
1
2
3
4
5


Probability of maturing
1.0
0.8
0.6
0.4
0.2
0.0
10
20
30
40
50
60
70
80
90
Length (cm)
S_{50}(1983)
1969
1983
S_{50}(1969)


Length (cm)
80
70
60
50
40
30
20
1965
1970
1975
1980
1985
1990
1995
2000
Cohort